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OENOTHERA LAMARCKIANA MUT. VELUTINA

HUGO DE VRIES

(WITH PLATE I)

One of the rarest mutations of *Oenothera Lamarckiana* is that in which those qualities are changed which constitute the characters of the twin hybrids *laeta* and *velutina*.<sup>1</sup> This is the more striking because in hybrid combinations these twins appear often and, as it seems, easily. But in the same way many other mutations, which apparently might reasonably be expected, have not as yet been observed and therefore must be assumed to be at least very rare. Why some mutations are common and others rare is still an open question.

From the behavior of the twin hybrids in crosses we may deduce that the mutant *velutina* must be in the main recessive to the parent species, and that the mutant *laeta* should be dominant over the *velutina*. If there were but one character involved, this would mean that the mutant *laeta* must be externally like *O. Lamarckiana*, and the same conclusion would have to be admitted if there were more characters indissolubly bound together. This being granted, the *laeta* could, of course, never be expected to appear as a mutant.

For some years, however, my cultures tend to show that the mutations observed in the group of the Oenotheras are far more compound phenomena than I was formerly inclined to assume. This also seems to be the case with the splittings which so often

<sup>1</sup> DE VRIES, HUGO, On twin hybrids. BOT. GAZ. 44:401-407. 1907.

occur after hybridization, and especially with those which appear in the first hybrid generation. If we apply this view to the twin hybrids *laeta* and *velutina*, the possibility is at once revealed that the components of this group of characters might not always be so indissolubly connected, and that some deviating combination of these qualities might still produce a mutant *laeta*, different from the type of *Lamarckiana*. As a matter of fact, a pure and complete mutant *velutina* has appeared in my cultures, but a *laeta* has never been seen as a mutant. In crossing this *velutina* with the parent species, however, twin hybrids arose, one of which may be designated as *laeta*, as will be shown later.

The question whether the characters of mutants and of hybrids among the *Oenotheras* are single or built up of a less or greater number of theoretically independent units now seems to be one of principal interest to me. Until now, however, the analysis of the qualities of the twin hybrids *laeta* and *velutina* has been difficult and unreliable on account of the presence of the hereditary qualities of their other parent. We can make inferences from these by comparing the twins issued from the crosses of different species with *O. Lamarckiana*, but we can hardly expect to get a complete analysis in this way. The mutant *velutina* is free from these specific admixtures, and therefore may afford a better material for experiments in this direction. I intend to study it from this point of view by means of a number of crosses, most of which I made during the summer of 1915, and shall give here only a description of the mutant itself, and of those hybridizations which give proof of its right to the name of *velutina*.

In order to avoid the confusion which might easily arise from the similarity of the names *O. Lamarckiana* hyb. *velutina* and *O. Lamarckiana* mut. *velutina*, I will give a synonym to the latter and call it *O. Lamarckiana* mut. *blandina*, or briefly *O. blandina*. In descriptions the use of this latter term will be obviously the easier. *O. blandina* has throughout its life and in all its organs a paler tinge than *O. Lamarckiana*.

*O. blandina* is, in all respects and at every stage of its evolution, strikingly different from *O. Lamarckiana* and easily recognizable. Its marks become visible with its very first leaves, when still in the

seed pans, about 4–6 weeks after sowing. At the time when the seedlings must be planted in larger boxes, their marks are fully reliable, even in hybrid mixtures. Their leaves are narrow and a pale yellowish green, whereas those of *O. Lamarckiana* are broad and a deeper green. As the rosettes increase the number and the size of their leaves, the differences between the two types are seen to increase also, and after some weeks more, when the young plants are ripe for transplanting into the garden, *O. blandina* is clearly a type of its own and can easily be counted off in the mixtures. In May the rosettes of *O. Lamarckiana* gradually become very stout, but those of *O. blandina* remain slender. The leaves are so narrow as not to touch each other regularly nor to cover the ground between them. They resemble those of *O. rubrinervis*, but lack the brittleness, the typical bending of the petiole and blade, and the specific color of this form. Moreover, they show a high degree of fluctuating variability in their color. This is always gray, on account of the hairiness of the surface, but it varies between a normal green and a more or less pale and yellowish tinge. The paler they are, the poorer they are in chlorophyll, and therefore the palest individuals soon begin to show a slower growth. They stay behind the others the more, the paler they are. These differences increase if the culture is densely planted, and even at the time of flowering the paler individuals may be seen to be much weaker and shorter than the others. In ordinary cultures, however, when the plants are at a distance of 20 cm. or more from their next neighbors, and grown in a well manured soil, these differences gradually disappear and are no longer visible when the first flowers open. In order to fertilize pale individuals beside the green ones, I had to mark them in early youth. From the self-fertilized seeds of the green ones the seedlings are on the average less pale than those of the paler parents, but the difference, although obvious and unmistakable on the beds in springtime, soon disappears as the summer begins. From time to time there is even a partial variability, such as, for instance, a green branch on a stem with pale leaves. This shows that there is no racial difference between the green individuals and the pale ones, even as in the cases of *Oenothera (Lamarckiana*  $\times$  *atrovirens*) *gracilis* and of *O. (Lamarckiana*  $\times$

*Hookeri*) *velutina*.<sup>2</sup> Since making these experiments (1912-1913) I have cultivated *O. blandina* so as to reduce the paleness of its leaves to the first youth of the rosettes, and to have no diminution of the individual strength of my seed-bearing specimens on account of it.

At the time of flowering the plants are much more slender than those of *O. Lamarckiana*, and are in their main features very much like the *velutina* hybrids of *O. biennis*  $\times$  *Lamarckiana* and of *O. Lamarckiana*  $\times$  *O. biennis* *Chicago*, and especially like the latter, with which in some instances they can easily be confounded. The leaves on the stem are narrow, reaching about two-thirds the breadth of those of *Lamarckiana* if compared by equal length. In the beginning they are folded along their midvein, but later they become flattened, and this curious character may then be seen only in the bracts of the inflorescence. The bubbles, which are so characteristic of the leaf blades of *O. Lamarckiana*, are absent in the mutant. I shall designate this lack of bubbles by the term "smooth."

The flowers of *O. blandina* are cup-shaped, whereas those of the parent species are more or less quadrangular. The size is the same, the color is as bright, and the stamens show no marked difference; the supply of pollen is very large in both cases. The stigma is widely spread out above the anthers, the distance being even somewhat larger in the mutant (1 cm. against 0.5 cm.). The flower buds are almost twice as thick in the mutant, more regularly and more deeply colored with red brown lines and spots, and much more hairy. This color and this hairiness extend over the tube of the flower and the ovary, and in a less degree over the top of the stem and the young bracts. The small free tips at the top of the flower bud are thick in *O. blandina* but thin in *O. Lamarckiana*. The differences of the fruits are small, except for the hairiness. The most striking character of *O. blandina*, however, is seen at the end of the flowering period, when the spikes are long and the lower fruits begin to ripen. At that period the spikes are very slender, with few fruits and long internodes, whereas on the spike of *O. Lamarckiana* the fruits are densely crowded. I counted the fruits

<sup>2</sup> Gruppenweise Artbildung. Berlin, 1913, p. 164, where *O. atrovirens* still bears the name of *O. cruciata* (fig. 73); and p. 116, fig. 46, for the twin hybrids of *O. Hookeri*.

on a length of half a meter in the middle part of the spike, at the end of September, and found 30 of them on *O. blandina*, but 75 on *O. Lamarckiana*, both on very vigorous annual specimens. From this the internodes of the spike are 1.7 against 0.7 cm., or more than twice as long as those of the parent species. The average numbers of flowers which open on a spike during an evening are inversely proportional to these figures. For many crosses I have castrated five successive flower buds of *O. Lamarckiana* on one day and pollinated them the next day, whereas the crossing of 5 flowers on a spike of *O. blandina* usually lasts 4 or more days, which makes quite a difference in the technical work.

Of course, there are a number of distinguishing points of less value, but their description would remain vague unless strict averages could be given; and since all characters are more or less dependent upon the conditions of soil and culture, it is doubtful whether even averages would be reliable. I shall return to this point in the description of the hybrids.

In comparing this description with that given in my book on *Gruppenweise Artbildung* for *O. (Lamarckiana) × O. biennis Chicago) velutina*, it will easily be seen that the two belong to the same type. In the garden, when groups of 10–30 plants are compared, this similarity is of course far more striking. It is at once clear that *O. blandina* must be a true and pure *velutina*.

If we now try to resume this description in such terms as to distinguish a number of probable units, the combination of which might constitute the type of *velutina*, I might propose the following: (1) slender stature; (2) long internodes of the flower spike; (3) leaves narrow, folded longitudinally and smooth, that is, without bubbles; (4) flowers cup-shaped; (5) hairiness of all organs; (6) abundance of red color in the younger parts. It is obvious, however, that some of these points may go together and depend upon one unit, but on the other hand it must be conceded that this list may be far from complete. Most of these assumed units are recessive to the corresponding qualities of *O. Lamarckiana*, but the smoothness is dominant over the bubbles, which are evidently due to a lack of growth parallel to the surface of the blade of the leaf. This enables us to separate smoothness from the larger part

of the other characters by means of crosses, as we shall see when dealing with the hybrids.

I shall now describe the origin of *O. blandina* and the pedigree of the race derived from it. As a matter of fact, this mutant did not arise directly from *O. Lamarckiana*, but through another mutant race as an intermediate. This was the fertile race of *O. lata* issued from an original fecundation of my normal *O. lata* by means of the pollen of *O. semilata*. This race is described in my book *Gruppenweise Artbildung* on pp. 256, 257. In the fourth generation of this race, issued from the seeds of 1904 sown in 1905, 1907, and 1908, three specimens of *O. blandina* were observed, two in 1907 and one in 1908. Besides these, the cultures consisted of specimens of *O. lata* and *O. Lamarckiana* in the usual proportions, and of other mutants such as *O. nanella*, *O. oblonga*, and *O. scintillans*. The size of the cultures, however, was too small to calculate percentage figures.

The full name of the new type, therefore, would be *O. Lamarckiana* (mut. 1888 *lata*  $\times$  mut. 1895 *semilata*) mut. 1907-8 *blandina*, leaving out the fecundation of the *lata* specimens of the pedigree by the pollen of *O. Lamarckiana*.

The second generation was derived separately from one mutant of 1907 and from that of 1908, both after guarded and artificial pollination. The seeds of the first mutant were sown in 1913 and gave a culture of 25 flowering individuals and 45 others which were pulled up shortly before flowering. Both groups were uniform, apart from the variation in the green color already mentioned. They were fully like the simultaneous culture of the third generation of the other strain, and for this reason this first line has not been continued.

The seeds of the mutant of 1908 were sown in 1912 and gave a culture of 67 flowering plants, all of which repeated the type of their parent. Besides these, I sowed part of the seed somewhat later in the season (June), and obtained a large group of rosettes of radical leaves, of which, however, only one survived our long, wet winter. This specimen flowered in 1913 on the main spike and on a number of branches, was very vigorous, but not strikingly stouter than the annuals of that summer.

In 1912 I saved the seeds of 4 self-fertilized plants separately. Two of them had been green from their first youth and the two others had been of a pale color in the beginning. The result was, in 1913, a small but distinct advantage of the two first sowings over the two latter sowings. I have chosen the first ones for the crosses to be described later on, and repeated this third generation in 1914 in order to give the plants more space and a better manured soil, and to compare such vigorous individuals with others growing in a dry and poor soil. The results of this comparison have been described elsewhere; they showed that the seeds produced by the two groups were different. Almost all the seeds of the strong plants contained a healthy germ, but among the seeds of the weaker individuals there were about 25 per cent of empty ones. The germination showed even a larger difference, giving about 80-90 per cent of seedlings for the normal seeds and only about 50 per cent for those of the weaker plants.<sup>3</sup> I shall return to this phenomenon in the second part of this article.

The fifth generation was derived, in 1915, from seeds of 4 self-fertilized individuals of 1914, chosen as the best ones among the stronger of the two groups. Sixty plants from one parent were planted in my experimental garden on good soil and with plenty of space, in order to be used for crosses. The remainder embraced about 3000 plants (between 600 and 800 from each parent), and were set out in another garden in order that the degree of mutability of this race might be studied. It was found to be rather small, although almost all of these plants have flowered and have been carefully tried at different stages of their evolution, from their germination to the time when their last flowers faded away in August and their first fruits ripened.

The result of these repeated inspections has been that 4 mutants, belonging to one type, were discovered, but that no other deviation could be observed. This gives a percentage figure of 0.1. If we compare this with the table given on p. 337 of my *Gruppenweise Artbildung*, we see that *O. blandina* falls into the group of those mutants (*O. nanella* and *O. rubrinervis*), the mutability of which has

<sup>3</sup> Über künstliche Beschleunigung der Wasseraufnahme in Samen durch Druck. Biol. Centralbl. 35:175. 1915. In this article *O. blandina* has been provisionally designated as *O. Lamarckiana* mut. nov. B.

become much smaller than that of the parent species, which latter is given there as 2.2 per cent. The transition of one or more unit characters into the inactive condition was considered there as the probable cause of this change, and the same conception may obviously be applied to our present case.

Although the mutability of *O. blandina* is thus seen to be very small, it does not follow that it is wholly absent for other mutations than the one mentioned. Casual mutations parallel to those of *O. Lamarckiana* may be expected to appear from time to time, either in the pure strains or after hybridizations with other, still less mutable, species. This has occurred once in my garden. Among the offspring of a cross between *O. blandina* and *O. Cockerelli*, a species from Colorado, an individual arose in 1915 which showed the marks of *O. lata* combined with those of *O. Cockerelli*, and agreed with the description given in my book (p. 254). It proves that the mutability of *O. blandina* into *lata* is not wholly absent.

The mutation from *O. blandina*, 4 specimens of which occurred in my culture of 1915, was a strikingly new type, quite different from all the mutations produced by *O. Lamarckiana* and its derivatives until now. It was distinguished at once by its linear leaves, which could be seen in the boxes before the young plants were planted out on the beds. The 4 mutants were brought into the glass-covered part of my garden, where 2 of them have flowered. The 2 others remained small, produced stems, but died in the fall before making any flower buds. Of the flowering specimens one was also small and therefore was not used as a seed-bearer, but the other reached about 1 m. in height, was very richly branched, and bore, from July to October, many hundreds of flowers and fruits. All these flowers had the same type, consisting of narrow petals instead of the large cordate ones of the parental form. The petals did not belong to the type called *cruciata*, inasmuch as they had not the least sign of the sepalody characteristic of *O. cruciata* and its allies. Their color was uniformly yellow, not differing from that of *O. Lamarckiana*. The breadth varied from 0.5 to 1.5 cm. for a length of 3 cm. The form was ovate, with some small indentations along the margin, and the tip was narrowed and more or less spirally twisted. This latter mark, which was best visible during

the time of the most abundant flowering, has induced me to choose for this mutation the name of *O. spiralis*.

As to the other marks, they were probably all evolved under the influence of the very narrow leaves, which could not produce food enough for very stout individuals or organs. The leaves measured 5–6 mm. in breadth by a length of 8–10 cm.; they were smooth (without bubbles) as in the parent, not folded longitudinally, only a little hairy, and dark green. The internodes were long, reaching 2 cm. or more, and the foliage was therefore thin and the whole habit slender. The flower buds were less hairy than in *O. blandina*, but more so than in *O. Lamarckiana*, and broader than would be expected from the narrow petals. The stigma was above the anthers, which contained a good supply of pollen, making artificial self-pollination and crossing quite easy. The fruits were rather thin, and somewhat smaller than those of *O. blandina*, a little more conical, and less hairy.

It should be pointed out that the origination in 4 specimens, one from one parent and the 3 others together from another parent, is analogous to the production of *O. blandina* itself, which arose in 3 specimens from one lot of seeds. It points to an internal condition of heritable mutability and suggests the expectation that under a better climate and with more suitable conditions of cultivation the number of simultaneous mutations in the same direction might increase sensibly.

CROSSES OF *O. BLANDINA* WITH OTHER SPECIES.—In order to give proof that *O. blandina* is really the mutant *velutina*, I made some crosses with such species as are known to split *O. Lamarckiana* and some of its other derivatives into the twin hybrids *laeta* and *velutina*. It is obvious that with the loss of the active qualities of *laeta* this capacity of undergoing a splitting must disappear. The mutant *velutina* corresponds to the latent or inactive condition of these qualities, and if combined with splitting species it must therefore give rise only to one of the twins, the hybrid *velutina*. In other words, the crosses with these species must be expected to produce no *laeta* but only *velutina* hybrids, and these must be exactly the same as the *velutina* issued from the corresponding crosses of *O. Lamarckiana*.

Under normal conditions the splitting of this latter species occurs in nearly equal groups of both the twins, but as a matter of fact the external circumstances are, with us, often such as to diminish the percentage of *laeta* quite sensibly. These deviations, however, have been amply studied in my work on *Gruppenweise Artbildung*; they show what size the cultures must be in order to prove the absence of *laeta*. I cultivated 60-80 offspring for each culture, and repeated the same cultures during 2 years, making on the average 140 specimens for each cross. The first year I compared them with the hybrids *laeta* and *velutina* derived from the corresponding crosses of my new dimorphic mutant *O. cana*,<sup>4</sup> which happened to be at hand in a complete set; but the second year I have sown the twin hybrids issued from crosses of *O. Lamarckiana* itself with the same species as were used for the crosses of *O. blandina*. The material is externally the same in both cases, and quite as good for the comparison, but in the latter instance the proof is a more direct one. I grew the hybrids of *O. blandina* and the control cultures side by side, and compared them from the beginning of germination in February until the ripening of the first fruits in September. The differences between the two twins of a cross are large and striking,<sup>5</sup> from their very first leaves, and it was therefore impossible that a *laeta* among the hybrids of *O. blandina* could have escaped observation. As a matter of fact, no single *laeta* appeared, although altogether over 500 hybrids were cultivated.

For these crosses I chose 2 heterogamic and 2 isogamic species, and made the combinations in both groups in the opposite directions, so as to use *O. blandina* twice as a pistil and twice as a pollen parent. I made these pollinations in 1913, in the third generation of my race, choosing the most vigorous individuals which had had a normal green color from their very youth. The crosses with the heterogamic species were *O. syrticola* Bartlett<sup>6</sup>  $\times$  *O. blandina* and *O. blandina*  $\times$  *O. biennis* Chicago. Those with the isogamic forms

<sup>4</sup> DE VRIES, HUGO, New dimorphic mutants of the Oenotheras. Bot. GAZ. 62: 249-280. figs. 5. 1916.

<sup>5</sup> For descriptions and photographs as well as for colored plates of the twins, see *Gruppenweise Artbildung*.

<sup>6</sup> This is the *O. muricata* L. of my *Gruppenweise Artbildung*.

were *O. Hookeri*  $\times$  *O. blandina* and *O. blandina*  $\times$  *O. Cockerelli*.<sup>7</sup> These combinations would have given the twins *laeta* and *velutina* if *O. Lamarckiana* had been used instead of *O. blandina*. Now, however, they gave only the hybrid *velutina*, showing that the splitting capacity of the parent species is absent in the mutant.

From these facts it follows that in *O. blandina* the *laeta* qualities of *O. Lamarckiana* are not only externally, but also internally, in the *velutina* condition. The former, therefore, is to be considered as a pure mutant *velutina*.<sup>8</sup>

I shall now describe the single crosses as briefly as possible.

*O. syrticola*  $\times$  *O. blandina* was made on 2 biennial plants of the first named species in July 1913, the pollen of a green *blandina* being used in the one case, and that of a pale green one in the other case. The seeds of the first one were sown in 1914, those of the other in 1915. Both of them gave cultures of 70 healthy offspring, making a total of 140, of which 25 and 10 specimens were allowed to flower and to ripen their fruits, after the others had been pulled up, in June, before flowering. They were compared in every month of 1914 with the twins of *O. syrticola*  $\times$  *O. cana*, and in 1915 with those from a cross of *O. syrticola*  $\times$  *O. Lamarckiana*, made in 1913 on a specimen of the same group of biennial plants as used for the cross with *O. blandina*. All of the 140 hybrids were evidently *velutina* and exactly like those of the control cultures.

*O. blandina*  $\times$  *O. biennis Chicago*.—This cross was made on two specimens of 1913, the pollen of the same parent plant being used in both of them. They gave uniform cultures of 60 and 80 plants, of which 25 and 10 were allowed to make long spikes of flowers and fruits. The others were annual plants also, but were thrown away in June, as soon as they reached a height of 30–40 cm., and showed their marks so as not to leave the least doubt concerning their *velutina* qualities. In 1914 I compared them with the hybrids of *O. cana*  $\times$  *O. biennis Chicago*, and in 1915 with those of *O. Lamarckiana*  $\times$  *O. biennis Chicago*, which I cultivated in the first generation

<sup>7</sup> For description and figures of these species see *Gruppenweise Artbildung*.

<sup>8</sup> Of course, other combinations, or combinations of the loss of the splitting capacity with other external marks must be admitted to be possible. As a matter of fact, such combinations occur from time to time, as, for example, in *O. oblonga*; see *Gruppenweise Artbildung*, p. 266.

as well as in the second, from another cross. The flowering individuals of all these crosses reached, in September, a height of more than 2 m., and all the *blandina* hybrids were, during all the stages of their evolution, like the *velutina* of the controlling cross.

*O. blandina*  $\times$  *O. Cockerelli*.—Seeds of only one cross of 1913 were tried, both parents being annuals. One part was sown in 1914, another in 1915; size of the cultures,  $60+80=140$  specimens, of which 25 and 21 flowered. One of the latter was the *lata* mutant previously mentioned. In June 1914, there was not the least doubt concerning the identity of all the 60 specimens with *O. (cana*  $\times$  *Cockerelli) velutina*, but in 1915 those young plants which had not been planted out in order to flower were a little too crowded. I therefore pulled out those which were indubitably *velutina*, and planted all the dubious ones on a separate bed, giving them just as much space as in ordinary cultures. About one-half of these (11 plants) flowered in September, but all of them displayed, at that time, the characters of *O. (Lamarckiana*  $\times$  *Cockerelli) velutina*, so as to leave no room for doubt. No *laeta* has appeared among the offspring of this cross.

*O. Hookeri*  $\times$  *O. blandina*.—Only one *Hookeri* was crossed in 1913 with one specimen of *blandina* of my race. The seeds gave 60 offspring in 1914 and 85 in 1915, of which 25 and 10 flowered. In the crosses of *O. Lamarckiana* and its derivatives with this Californian species, the *velutina* have almost the features of *O. Hookeri* itself, showing only a small influence of the other parent. I compared my hybrids in both years with first generation hybrids, using for the comparison both the reciprocal crosses of *O. cana* of 1913 in one year and the hybrids of a cross *O. Hookeri*  $\times$  *Lamarckiana* of 1909 in the next year. Although the specimens, which were not allowed to flower, made stems of only a few centimeters, or stayed in the conditions of rosettes of radical leaves, the type of *O. Hookeri* was strongly pronounced in them. All of them had the long narrow leaves of *velutina*, and no *laeta* occurred in the whole culture of 145 plants.

Resuming these details, we see that 565 hybrids of *O. blandina* with splitting species have been studied, and that all of them bore the unquestionable features of the *velutina* of the corresponding crosses of *O. Lamarckiana* and of *O. cana*.

CROSSES OF *O. BLANDINA* WITH *O. LAMARCKIANA*.—If the *laeta* qualities have become latent and inactive in *O. blandina*, we should expect that this mutant would have acquired the property of splitting itself these qualities in *O. Lamarckiana*. The confirmation of this expectation must obviously strengthen the conclusion from which it started. And since *O. nanella* and other mutants may give rise to the same hybrid twins as the parent species, we may expect *O. blandina* to split them also. I made both the reciprocal crosses with the parent species and one with the dwarf, and all 3 cases have corroborated my conception. I made the crosses in 1913 in the third generation of my race, and cultivated the first generation in 1914, repeating it in 1915. The splitting occurred in all 3 cases as expected, giving nearly equal groups of the two types. One of these types exactly corresponded to *O. blandina* itself; in comparing it from its first youth up to the time of flowering and fruiting, I could not discover any difference. This one should be considered as the *velutina*, therefore, and will be called *O. (Lamarckiana*  $\times$  *blandina*) *velutina* a.s.o. The other type was evidently a *laeta*. During some stages of its evolution it was almost wholly like *O. Lamarckiana*, but later it changed its appearance and displayed some of the characters which usually distinguish the different forms of the hybrid *laeta* from their parents. For this reason I shall call it *O. (Lamarckiana*  $\times$  *blandina*) *laeta*, or briefly *O. blandina laeta*, implying by this name only the presence of one or more characteristics of the *laeta* type, but not necessarily all of them.

According to the species which determine the splitting in *O. Lamarckiana*, the types of hybrid *laeta* may be divided into two groups. One of them is small-flowered and ordinarily tall, corresponding to the *rigida* type described and figured in my book (pp. 73, 80, 81). To this type appertain the *laeta* produced by *O. biennis*, *O. muricata*, *O. Cockerelli*, and *O. biennis Chicago*. The other type has large flowers; it embraces only the *O. (Hookeri*  $\times$  *Lamarckiana*) *laeta* and its reciprocal. The flowers have the same size in both parents, and therefore this size is not changed in the hybrids. In the cross of *O. Lamarckiana* and *O. blandina* the same rule prevails, the flowers of the hybrid being not rarely even somewhat stouter than those of the parents.

*O. blandina laeta* shows the greatest affinity to *O. Hookeri laeta*, not only in the flowers, but also in other respects, as, for example, in the stature at the time of flowering, which in both hybrids comes much nearer to that of *O. Lamarckiana* than any of the small-flowered hybrid *laeta*. Far more interesting, however, is the similarity in its behavior in the second generation, after *self-fertilization*. The *Hookeri laeta* are the only *laeta* as yet known to split; all *laeta* of other extraction and all the *velutina* as yet studied give a uniform progeny. But the *Hookeri laeta* split in every generation into *laeta* and *velutina* which are exactly like the original twins.<sup>9</sup> The same phenomenon is seen in *O. blandina laeta*, although as yet I have only cultivated one second generation from one cross. This was *O. blandina*  $\times$  *O. Lamarckiana*, made in 1913. The first generation in 1914 gave 59 per cent *velutina* and 41 per cent *laeta*, and the progeny of the latter split into the same two types in 1915, giving 67 per cent *velutina* and 33 per cent *laeta*. Why the large-flowered *laeta* should split, but the small-flowered type remain constant, is a question which will have to be studied later.

*O. blandina laeta* has been, throughout its whole evolution, exactly the same type in the 3 crosses already mentioned, and whose progeny I cultivated in both years side by side. In the seed pans and the transplanting boxes the young plants are almost exactly like *O. Lamarckiana*, resembling this form far more than any of the hybrid *laeta* do. This condition prevails until the beginning of flowering, during which period the leaves of the stem are somewhat broader and less covered with bubbles than in the parent species. This difference is then seen to increase gradually and becomes evident in the lower bracts of the inflorescence, which are broad, especially at their base, smooth, and wholly or almost without bubbles. As the spike develops, the difference from the parental type becomes greater. The fruits are less crowded and somewhat stouter, and the plants gradually reach a greater height than specimens of *O. Lamarckiana* planted at the same time and under the same conditions. Although the differences are still small, apart from the smoothness of the leaves, the plants of *O. blandina laeta* cannot be mistaken for *Lamarckiana* during all the time of flowering, which may last more than 2 months.

<sup>9</sup> See the pedigrees in *Gruppenweise Artbildung*, p. 131.

It seems probable that the increased breadth and the diminished bubbles of the higher leaves of the stem and of the bracts of the inflorescence are expressions of a single change, which must consist in a thorough stretching of the blade parallel to its surface. If this be so, we may conclude that the bubbles, which are so characteristic of *O. Lamarckiana*, are due to some deficiency in this stretching and thereby constitute a recessive character. If this conclusion be granted, the smoothness of the leaves of *O. blandina* must be dominant in its crosses with *O. Lamarckiana*, and in this way be transferred to both of its twins, causing the one to be a *laeta* instead of a pure *Lamarckiana*. We are thereby provided with a beginning of an experimental analysis of the marks of mut. *velutina*, as already discussed.

Here I might insert some considerations concerning the mutative origin of *O. blandina*. We have seen that *O. Lamarckiana* and *O. nanella*, when crossed with this new form, repeat its characters in part of the offspring. In the same way a mutant *velutina* may be produced by the conjugation of a mutated sexual cell with a normal one. Thus it is not necessary to assume the accidental meeting of two mutated gametes, which would obviously make the chance of the mutation occurring very much smaller still. It is sufficient to suppose that only the female elements of the original *O. laeta* have mutated in this way, although we cannot know whether this change might not have taken place in the male cells. And since *O. blandina* behaves as an isogamous species, both hypotheses seem to be equally probable. In both cases mutants of the *laeta* type should be expected to appear also, but as they would be very rare and not discernible in the beginning from the *Lamarckiana* specimens which always develop out of a part of the seeds of *O. lata*, they would surely have been overlooked in the years 1907–1908, when the mutation into *blandina* occurred.

I shall now give a more detailed description of my experiments. The crosses were made in 1913 and the first generation was cultivated twice for every cross, once in 1914 and once in 1915.

*O. blandina*  $\times$  *O. Lamarckiana*.—A biennial specimen of the latter form was chosen and its pollen placed on the stigma of two individuals of the thoroughly green type of *O. blandina*. The seeds of one cross were sown in 1914, and those of the other in 1915.

The first culture consisted of 23 *laeta* and 34 *velutina*, making a total of 58, with 41 per cent *laeta*. In 1915 the figures were 46 *laeta* and 39 *velutina*, or 54 per cent *laeta* in 85 specimens. Although the size of the cultures was small, they evidently point to a division in nearly equal groups. The two types were clearly different from the beginning and could easily be counted out in June before the production of the stems. In 1915 I separated them in March, at the time of planting into the boxes, in order to control my estimate later on, and in April planted the *laeta* in one group and the *velutina* in another half of the bed. In 1914 I had 25 and the following year 10 flowering plants, half of which belonged in each case to the *laeta* type and the other half to the *velutina* type. The *laeta* have already been described; the *velutina* were in no respect and at no time different from ordinary *O. blandina*.

The second generation from seed of one of the *velutina* plants embraced 30 flowering and 40 younger specimens, all of which exactly repeated the marks of their parent. From the seeds of one self-fertilized *laeta*, however, I got the splitting group already described. Its two types were the same as in the previous generation. I recognized the splitting in the seed pan, but counted them only in June after planting out 15 *laeta* and 15 *velutina*. All in all I had 80 plants, of which 26 were *laeta* and 54 *velutina*, or 33 per cent *laeta*, which is somewhat less than in the first generation. All the 30 specimens of the bed richly flowered and ripened their first fruits before being thrown away.

*O. Lamarckiana*  $\times$  *O. blandina*.—A biennial plant of the species was crossed in 1913 with a green individual of the mutant. The seeds were sown partly in 1914 and partly in 1915. They gave the same two types as in the reciprocal cross. During the whole lifetime there were no visible differences. In the first year I had 60 plants with 22 per cent *laeta*, and in the second year 108 specimens with 25 per cent *laeta*; the remainder were *velutina*. Of these, 25 and 10 flowered, in about equal groups for both types, having been recognized and sorted out at the time of planting. The other plants were cultivated till the end of June.

*O. blandina*  $\times$  *O. nanella*.—Two green individuals were fertilized in 1913 by the pollen of my race of *O. Lamarckiana* mut.

*nanella*; the seeds of the one were sown in 1914 and of the other in 1915. There were no dwarfs in this first generation, but only *laeta* and *velutina*, which were just like those of the crosses already described. I had 90 and 72 plants, with 74 and 67 per cent *laeta*. There were 25 and 10 flowering plants belonging equally to the two groups; the others were large rosettes in June.

If we compare the percentages of *laeta* given with one another we find for *O. blandina*  $\times$  *O. Lamarckiana* 41 and 54 per cent, for the reciprocal cross 22 and 25 per cent, and for the experiment with the dwarfs 74 and 67 per cent; finally, for the second generation of the first cross 33 per cent. The average of all these figures is 45 per cent *laeta*, which comes as near to equality of the two groups as may be expected. The deviations from this mean are probably due mainly to the choice of the parents and to their cultural conditions.

*O. rubrinervis*  $\times$  *O. blandina*.—Besides the 3 crosses already mentioned and discussed, I have also made the two reciprocal crosses with my race of *O. rubrinervis*. In the first generation they split in the same way, the only difference being that instead of the *laeta* another type arises. This is the *subrobusta*, which appears in the hybrid splittings of *O. rubrinervis* with other derivatives of *O. Lamarckiana*, as described in my *Gruppenweise Artbildung*. No differences were observed, although the comparison lasted from germination till the ripening of the fruits. The other type was the same as in the crosses already dealt with, and exactly like the parental type of *O. blandina*.

The cross was made in 1913 between an individual of my pure race of *O. rubrinervis* and a specimen of the third generation of *O. blandina*. One part of the seeds was sown in 1914 and another in 1915. In the first year I had 60 plants with 32 per cent *blandina*, and cultivated 18 *laeta* and 7 *blandina* until the ripening of their fruits. In the last named year I had 77 specimens, of which 61 per cent were *blandina* and of which 5 *laeta* and 5 *velutina* were left to flower. All in all, the cultures embraced 137 plants, with 45 per cent *blandina*. The others were all *subrobusta* and not different from the *subrobusta* cultures of those years resulting from other crosses.

*O. blandina*  $\times$  *O. rubrinervis*.—For this cross I used two specimens of *O. blandina* of the third generation in 1913, the one being a pale green and the other a normal color. In 1914 each of the cultures embraced 60 plants, of which 25 flowered. The percentages for *blandina* were 48 for the green, but only 20 for the pale parent. For this reason I repeated the latter culture in 1915 and obtained from 70 plants 47 per cent *blandina*. The types of *subrobusta* and *velutina* in these cultures were exactly the same as those from the reciprocal cross.

The percentages given are obviously of the same type as those for the splitting into *laeta* and *velutina* and come as near to equality for the two types as may be expected under ordinary conditions of cultivation. I propose to grow the second generation next summer.

**THE VIABILITY OF THE SEEDS OF *O. LAMARCKIANA* MUT. *VELUTINA*.**—Besides the external differences between our new mutant and the parent species, there is another mark which lends a high interest to the new form. This is found in the seeds. The seeds of *O. Lamarckiana* differ from those of almost all other species (with the exception of *O. suaveolens*) in containing a large proportion of empty grains, even under the most favorable conditions of life. More than one-half of the seeds have no germ at all, although externally they are, as a rule, not distinguished from the normal ones. RENNER<sup>10</sup> has studied the development of these empty seeds and found that their germ is fecundated and undergoes one or two cell divisions, but then stops and dies off. He considers this phenomenon as a hereditary character of the species. It runs parallel, in this respect, to the rudimentary ovules described by GEERTS, which are characteristic of the whole group of the *Oenotheras*. Besides this type of empty seeds a less or larger number usually occur which stop their development at a much later stage. The proportion of these can be diminished by a better culture, and therefore they may be considered as a result of the crowding of the seeds in the capsules, combined with the limited amount of nourishment available for them.

Our new mutant *velutina* produces hardly any abortive seeds, at least under normal conditions of culture. I tried the seeds from

<sup>10</sup> RENNER, O., Befruchtung und Embryobildung bei *Oenothera Lamarckiana*. Flora 7:115-150. 1914.

purely pollinated capsules of 4 specimens of my culture of 1915, which was the fourth generation of my race. I took them carefully out of the fruits, mixed those of 5 successive capsules of the same spike, and counted 200 grains from each lot. I soaked them in water, pushed this into their seed coats by means of a pressure of 8 atmospheres for about 24 hours, and afterward laid them out to germinate in small glass tubes in a stove at 30° C.<sup>11</sup> Within 6 days the larger part of the seeds germinated, giving percentages of 85, 84, 73, and 70 for the 4 lots. I then opened the remaining grains and found fully developed germs in almost all of them. The percentage of germs, being the sum of the two trials, came to 99, 96, 96, and 93, and there is no doubt that if they had been left in the stove for a longer time, almost all of the resting germs would have shown signs of germination.

The proportion of rapidly germinating grains and that of empty ones depend in a high measure upon the external conditions of life. During the summer of 1914 I cultivated 2 lots of individuals from seeds of the same parent plant, giving to one of them the ordinary favorable conditions of my garden, and keeping the others in a dry soil without manure. The seeds of the 2 most vigorous specimens of both lots, taken from self-fertilized capsules, were tried. They contained 99 and 99 per cent of germs for one group, but only 72.5 and 73.5 per cent for the other group. The same effect was shown in the amount of grains which germinated within the first 6 days. The figures were 80–88 per cent in one case and 53 per cent in the other case.<sup>12</sup>

The loss of the hereditary property of producing about 50 per cent of empty grains constitutes a latent mutation accompanying the visible changes in the external structure. The same loss accompanies the mutation into *gigas*, *rubrinervis*, and some newer mutants, but does not occur in such cases as those of *O. lata*, *O. scintillans*, *O. cana*, and others (see footnote 4).

<sup>11</sup> This method has been followed in all the experiments to be described in the text. It is described in the following papers: The coefficient of mutation in *Oenothera biennis* L. Bot. GAZ. 59: 190–194. 1915; and in Über künstliche Beschleunigung der Wasseraufnahme in Samen durch Druck. Biol. Centralbl. 35: 161–176. 1915.

<sup>12</sup> Biol. Centralbl. 35: 174–175, where *O. blandina* was provisionally indicated as mut. nov. *B*.

I made a series of crosses in order to study the nature of this latent mutation of *O. blandina*. They led to the discovery of some points which seem to deserve a more thorough study than I could give them until now.

In the first place, it is to be expected that in crosses with those species which do not produce such empty seeds the high figures of both parents will simply be repeated. I tried these cases, determining the amount of normally developed germs in lots of 200 seeds each, after the method already described. I made the crosses in 1914 and 1915, and in most cases in both the reciprocal directions. The seeds were taken from 5 successive fruits, and carefully prepared so as not to lose any small grains. The results are given in table I.

TABLE I

CROSS	PERCENTAGE OF GERMS*		
	Cross	Cross	Reciprocal
<i>O. biennis</i> × <i>blandina</i> .....	99	—	91
<i>O. biennis</i> Chicago × “ .....	95	89	94
<i>O. Cockerelli</i> × “ .....	99	95	87
<i>O. Hookeri</i> × “ .....	94	91	—
<i>O. syrticola</i> × “ .....	87	83	—

\* The dash (—) means that the cross has not been tried.

In some instances I cultivated the first generation of the hybrids in 1915 and tried their seeds after self-fertilization. I got almost the same figures: *O. blandina* × *Chicago* 86 per cent, *O. Hookeri* × *blandina* 97 per cent, and *O. syrticola* × *blandina* 93 per cent.

In trials with other species the hereditary property of *O. Lamarckiana* of making germs in only one-half of its seeds is recessive to the normal condition of producing almost only normal grains. It behaves in the same way in crosses with *O. blandina*. The results are given in table II.

Of course it is to be expected that those mutants which themselves give high percentages after self-fertilization will do the same in their crosses with the *velutina* mutant (table III).

The crosses were made in 1915. *O. rubrinervis* is the same strain as used in my *Gruppenweise Artbildung*. *O. erythrina* is a new mutant from *Lamarckiana*, of the type of the hybrid form *subrobusta* of that book; and *O. deserens* is a mutant from *O. rubri-*

*nervis*, originated through the loss of the typical red color, but without change in the brittleness of the stem. These new mutants will have to be dealt with in another article.

TABLE II

CROSS	CULTURE	PERCENTAGE OF GERMS	
		Cross	Reciprocal
O. <i>blandina</i> × <i>Lamarckiana</i> .....	1914	94	—
“ × “ .....	1915	97	95
“ × <i>nanella</i> .....	1915	99	—
O. <i>Lamarckiana</i> × <i>blandina</i> .....	1914	90	—

The most interesting question in this situation, however, is that concerning the seeds of the first generation of the crosses between *O. Lamarckiana* and *O. blandina*. I made the crosses in

TABLE III

CROSS	PERCENTAGE OF GERMS	
	Cross	Reciprocal
O. <i>blandina</i> × <i>rubrinervis</i> .....	91	97
“ × <i>erythrina</i> .....	99	—
“ × <i>deserens</i> .....	99	100

1914, cultivated the hybrids in 1915, and tried their self-fertilized seeds during the winter. From each of the 3 crosses I had 5 vigorous specimens of the *laeta* type, and an equal number of the *velutina* type. I shall deal with the *laeta* first (table IV).

TABLE IV

SELF-FERTILIZED SEEDS OF *laeta* SPECIMENS OF THE FIRST GENERATIONS

Cross	Percentage of germs				
O. <i>Lamarckiana</i> × <i>blandina</i> .....	98	98	97	96	95
O. <i>blandina</i> × <i>Lamarckiana</i> .....	96	96	95	92	36
“ × <i>nanella</i> .....	96	96	43	41	39

The 3 crosses may be taken as instances of one type and combined on this ground. We see that a splitting occurs, 11 individuals having the high percentages of the one parent, and 4 others

having the low figures of *O. Lamarckiana*. This splitting may be considered, therefore, as amphiclinous,<sup>13</sup> 73 per cent of the hybrids belonging to the one and 27 per cent belonging to the other parental type. The splitting is analogous to that of the cross *O. Lamarckiana*  $\times$  *nanella*, which gives, under ordinary circumstances, in the first generation about 78 per cent tall and 22 per cent dwarfish specimens. It must be pointed out, however, that here the germs, which belong to the next generation, are dealt with as a mark of the first generation. In this respect they may be compared with the rudimentary ovules of GEERTS, which are not fertilized.

I tried also the *blandina* plants of the same crosses, but had fertilized only two specimens of each, which is too few to study this phenomenon. I found 77 and 69 per cent, 67 and 60 per cent, and 71 and 70 per cent of good grains among their seeds. It is remarkable that all of these plants had about the same figure, which is far less than that of the specimens of the pure race of *O. blandina* (about 95 per cent), but a splitting did not show itself.

The same difference as between the *laeta* and extracted *velutina* was shown by the *subrobusta* and the *velutina* from the crosses with *O. rubrinervis*. I found the figures as given in table V.

TABLE V

Cross	Hybrid	Percentage of germs		
		subrobusta	“	—
<i>O. rubrinervis</i> $\times$ <i>blandina</i> . . . . .	subrobusta	97	96	—
<i>O. blandina</i> $\times$ <i>rubrinervis</i> . . . . .	“	96	96	96
<i>O. rubrinervis</i> $\times$ <i>blandina</i> . . . . .	blandina	70	68	—
<i>O. blandina</i> $\times$ <i>rubrinervis</i> . . . . .	“	80	75	—

It is possible, however, that this difference is only an effect of the higher exigencies of the plants of the type of *blandina*, since we have already seen that their amount of good grains is easily diminished by an unfavorable culture. Moreover, this character is not a constant one, for in trying the *blandina* plants of the second generation I found their contents of normal embryos complete, no single empty grain being found in lots of 200 seeds of two such plants.

<sup>13</sup> Über amphikline Bastarde. Ber Deutsch. Bot. Gesells. 33:461-468. 1915.

It is necessary, of course, to study the progeny of the *laeta* plants with a high and of those with a low percentage figure. Until now, however, I have had only an opportunity to study the offspring of one *laeta* of the first type, since I happened to have fertilized only that one in 1914. Its seeds contained 96 per cent of germs. I cultivated 15 specimens of *laeta* from these seeds, and found, for self-fertilized seeds of each of them, percentages between 91-97, with a mean of .95. In this instance, therefore, the high percentage seems to be constant.

The main result of this inquiry is that *O. Lamarckiana* mut. *velutina* has lost the property of the parent species of producing about one-half of empty grains, that this property is recessive to the normal production of almost only good grains, and that a splitting is observed in the first generation, which seems to follow the type of amphiclinous hybrids, as in the case of *O. Lamarckiana*  $\times$  *O. nanella*. A further study is required to elucidate these points, especially the behavior of the seeds as a mark of the generation which produces them.

### Summary

1. *O. Lamarckiana* mut. *velutina* = *O. blandina* arose from my family of *O. Lamarckiana* mut. *lata*  $\times$  *semilata* among seeds of the third generation saved in 1904, in 3 specimens. Of one of these I cultivated a second generation and of one of the others 4 successive generations, embracing together over 3000 plants.

2. All these plants were exactly alike with the exception of 4 mutants which constituted a new type, *O. spiralis*. The mutation coefficient was 0.1 per cent, or about the same as for *O. rubrinervis* and *O. nanella*, and much smaller than that for *O. Lamarckiana*.

3. For the appearance of the original mutation only one sexual cell needs to be mutated, since in combining with a normal gamete it may give rise to *O. blandina*, as is shown by the splitting of both the reciprocal crosses of this form with *O. Lamarckiana*. The splitting goes into nearly equal groups of specimens like *O. blandina* and of *laeta*.

4. *O. Lamarckiana* mut. *velutina* resembles the hybrids of the type of *velutina* so much as to be considered one of them. Among

them it is the most like *O. (Lamarckiana)×O. biennis Chicago*) *velutina*, without the marks of the second parental species, however. It is slender, with long internodes in the spike, and with flowers as large as those of *O. Lamarckiana*.

5. *O. Lamarckiana* mut. *velutina* is distinguished from its parent species in a very striking character. It has lost the property of producing about one-half of empty grains; almost all of its seeds contain healthy and well developed germs and germinate easily. This new quality is dominant over that of the parent. It is the same as in almost all the older species of the genus.

6. Moreover, *O. mut. velutina* is distinguished from *O. Lamarckiana* at least in one other dominant character, the smoothness of its leaves at the time of flowering. Secondly, it is distinguished in quite a number of characters, which seem to be more or less independent of one another, namely, slender stature, long internodes of the flower spike, narrow and longitudinally folded leaves and bracts, and cup-shaped flowers. Besides these, the richness in red color and the hairiness of all organs, especially in their youth, are very striking marks.

7. In crosses with those species which split *O. Lamarckiana* and some of its other derivatives into the twin hybrids *laeta* and *velutina*, the *O. mut. velutina* produces only hybrids of the *velutina* type.

8. In crosses with *O. Lamarckiana* and *O. nanella*, these forms are seen to be split by *O. mut. velutina* into twin hybrids, which correspond to the twins produced by other species with them, but which, of course, lack the characters of those other parents. The twins of *O. blandina* may be considered as pure *laeta* and pure *velutina*, therefore, the former having smooth leaves and bracts in the summer, the latter being identical with *O. blandina* itself.

9. The study of our new mutant reveals the existence of at least two recessive characters in *O. Lamarckiana*, namely, the bubbles of the leaf blade and the presence of typical empty seeds.

BOTANIC GARDEN  
AMSTERDAM

#### EXPLANATION OF PLATE I

At the right, *Oenothera Lamarckiana* mut. *velutina* (*O. blandina*); at the left, *O. blandina* mut. *spiralis*.



DEVRIES on OENOTHERA